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CONCEPTS & THEORY

How spatial scale shapes the generation and management of multiple ecosystem services

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Citation: Lindborg, R., L. J. Gordon, R. Malinga, J. Bengtsson, G. Peterson, R. Bommarco, L. Deutsch, Å. Gren, M. Rundlöf, and H. G. Smith. 2017. How spatial scale shapes the generation and management of multiple ecosystem services. Ecosphere 8(4):e01741. 10.1002/ecs2.1741

Abstract. The spatial extent of ecological processes has consequences for the generation of ecosystem services related to them. However, management often fails to consider issues of scale when targeting ecological processes underpinning ecosystem services generation. Here, we present a framework for conceptualizing how the amount and spatial scale (here discussed in terms of extent) of management interventions alter interactions among multiple ecosystem services. First, we identify four types of responses of ecosystem service generation: linear, exponential, saturating, and sigmoid, and how these are related to the amount of management intervention at a particular spatial scale. Second, using examples from multiple ecosystem services in agricultural landscapes, we examine how the shape of these relationships can vary with the spatial scale at which the management interventions are implemented. Third, we examine the resulting scale-dependent consequences for trade-offs and synergies between ecosystem services as a consequence of interventions. Finally, to inform guidelines for management of multiple ecosystem services in real landscapes, we end with a discussion linking the theoretical relationships with how landscape configurations and placement of interventions can alter the scale at which synergies and trade-offs among services occur.

Key words: agricultural landscapes; ecosystem function; management interventions; multifunctional landscape; scale mismatch; spatial extent; synergies; trade-offs.

Received 14 January 2017; accepted 20 January 2017. Corresponding Editor: Debra P. C. Peters.

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Introduction

Spatial scale is a crucial aspect of ecology and ecosystem functioning (Wiens 1989, Levin 1992, Peterson et al. 1998). Despite this, scale issues are often insufficiently considered in ecosystem service assessments (Chan et al. 2006, Fisher et al. 2009), reducing the relevance of assessments for resource management decisions and policy development since ecological scale mismatches are left unrecognized (Cumming et al. 2006, Daily et al. 2009). Consequently, clarifying the effects of management at different spatial scales has been identified as an important issue for ecosystem service science (Carpenter et al. 2006, Power 2010, Prager et al. 2012).

Management of ecological processes promoting ecosystem services can be undertaken at different spatial scales from local to global. Final ecosystem services, like food and climate regulation, are underpinned by intermediate ecosystem services (e.g., pollination, and nutrient retention) in what has been described as a cascade of ecosystem processes (Potschin and Haines-Young 2011, see also Fischer et al. 2009). The ecosystem processes in the cascade operate at different spatial scales, with consequences for how to manage them best; that is, interventions to promote intermediate services in the cascade can reshape the supply of final services. For example, an intermediate service such as carbon sequestration to soils primarily depends on ecological processes operating at small spatial scales (Barrios 2007), and can be managed accordingly. However, the translation into climate regulation resulting from a reduction in CO_2 in the atmosphere is made at global scales necessitating management at large spatial scales to avoid under-provision of ecosystem services (Fisher et al. 2009).

The mismatch between the scales at which final services are utilized in relation to where they are generated, has received considerable attention because such scale mismatches result in an under-supply of ecosystem services (Swinton et al. 2007, Lant et al. 2008). However, less attention has been paid to scale mismatches affecting the management of intermediate ecosystem services. Intermediate services generated by species in meta-communities can be affected by processes occurring at landscape or even larger spatial scales (Leibold et al. 2004). For example, interventions to increase pollination implemented at a very small scale may not sufficiently enhance pollinator populations to have any effect on the pollination service (Gabriel et al. 2010, Stallman 2011).

Scale mismatches have been discussed for single services (e.g., Sandel and Smith 2009), but are not well understood for multiple interacting services, where each service has a different scale-dependent relationship between management and its flow (Bennett et al. 2009, Fisher et al. 2009). For instance, a management intervention performed at a specific scale intended to support a specific ecosystem service could affect other services positively. Yet, this synergy might disappear or even turn into a trade-off if the intervention is performed at another scale. An example is no-till management of agricultural fields, which can increase carbon sequestration and yield. However, when applied at a large scale in Australia, the positive effect on yield was reversed because it led to high populations of mice (Singleton and Griffiths 2011). Thus, managing landscapes for multiple ecosystem services is complex and likely to create trade-offs and synergies among services (Bennett et al. 2009, Raudsepp-Hearne et al. 2010).

Here, we develop a conceptual framework to address scale-dependent relationships between management and the generation of ecosystem services and related challenges. We focus on intermediate ecosystem services because they equal the ecosystem processes underpinning the final services and are the ones mostly targeted in management interventions. We identify scale-dependent trade-offs and synergies in service management, and apply this framework to agricultural landscapes where management is critical to ensure the flow of multiple ecosystem services (Foley et al. 2005). First, we propose theoretical functions of the relationships between ecosystem service generation and the amount of management intervention provided in a given landscape. We discuss how ecological processes can affect the shape of these curves. Second, to disentangle the effect of spatial scale (extent) from the amount of interventions, we analyze how the shape of these relationships varies with spatial scale for some relevant farmland interventions. By distinguishing between spatial extents of a management intervention, for example, within a small field (<1 ha) or within a larger landscape (>1000 ha), and the amount of interventions in the managed area, it is possible to identify trade-offs and synergies among ecosystem services in relation to management interventions at multiple scales. Finally, we discuss scale mismatches between the spatial scale of ecological processes in the ecosystem service cascade and the scales at which they need to be managed.

Functional Form of Ecosystem Service–Intervention Relationships

Scale dependencies in ecosystem services generation can be examined by studying how

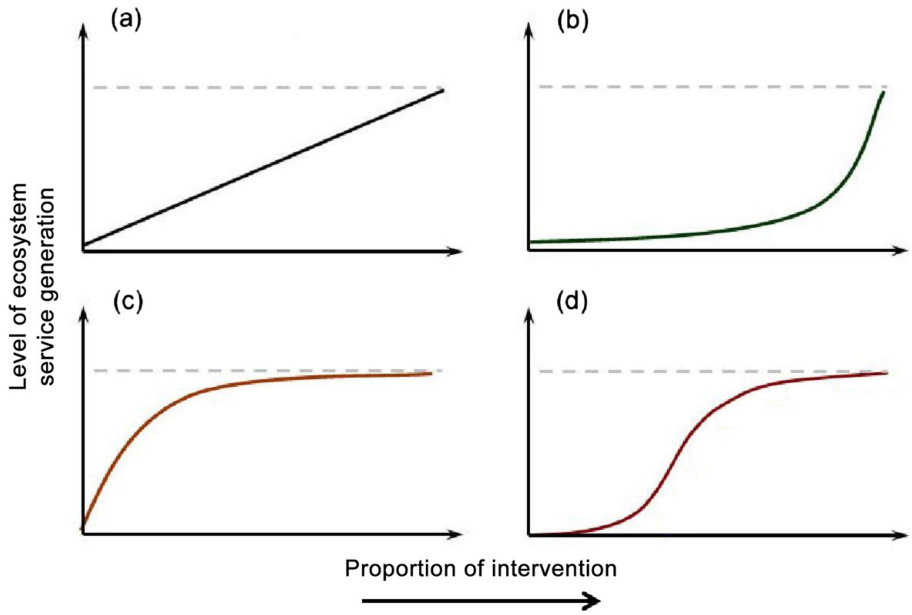

Fig. 1. Hypothetical relations between ecosystem service provision and the amount of management intervention. The *y*-axis shows the level of service produced, and the *x*-axis shows the amount (proportion) of intervention needed to produce the service in question. (a) linear—the provision of the ecosystem service is directly linearly related to the amount of intervention; that is, the service production will be directly affected by even a local intervention; (b) exponential curve—the amount of management intervention is not linearly related to ecosystem service production, but needs a certain amount of intervention to actually be produced; (c) saturating—the production of the service will reach an asymptote; that is, the target level of ecosystem service provision will not increase with more interventions; (d) sigmoid relationship combining b and c (see *Functional Form of Ecosystem Service—Intervention Relationships* for examples). The dashed horizontal line represents the target level of service provision.

these are affected by management interventions applied at different spatial scales. The concept of scale has been used to refer to grain size, sampling unit, density, and extent (Scheiner et al. 2000). Here, we focus on how the *amount* of intervention (expressed as density) affects the generation of services when applied at areas of different *extent*. To this end, we first propose hypothetical relationships between level of ecosystem service generation and the amount of management intervention irrespective of the spatial extent (Fig. 1). However, the shape of the curves describing these relationships can change with the spatial scale at which interventions are applied. We therefore continue in Fig. 2 by examining how specific interventions in agricultural landscapes affect the generation of sets of ecosystem services when applied at different spatial extents (scales).

Imagine a landscape into which we introduce an intervention intended to support a certain organism or process that produces a particular intermediate ecosystem service. It could be expected that the level of the intended service increases monotonically with the amount of the intervention. Although some ecosystem services can increase linearly (strictly additive and non-saturating) with the amount of the intervention (Fig. 1a), others show various non-linear forms. Generation of these services initially increases exponentially with the amount of intervention, due to, for example, ecological threshold effects (Fig. 1b). For many ecosystem services, there will also be an asymptotic relationship, because ecological processes underpinning the service are limited by other factors at high levels of the intervention (Fig. 1c). Combining thresholds and saturation effects results in a sigmoid relationship (Fig. 1d).

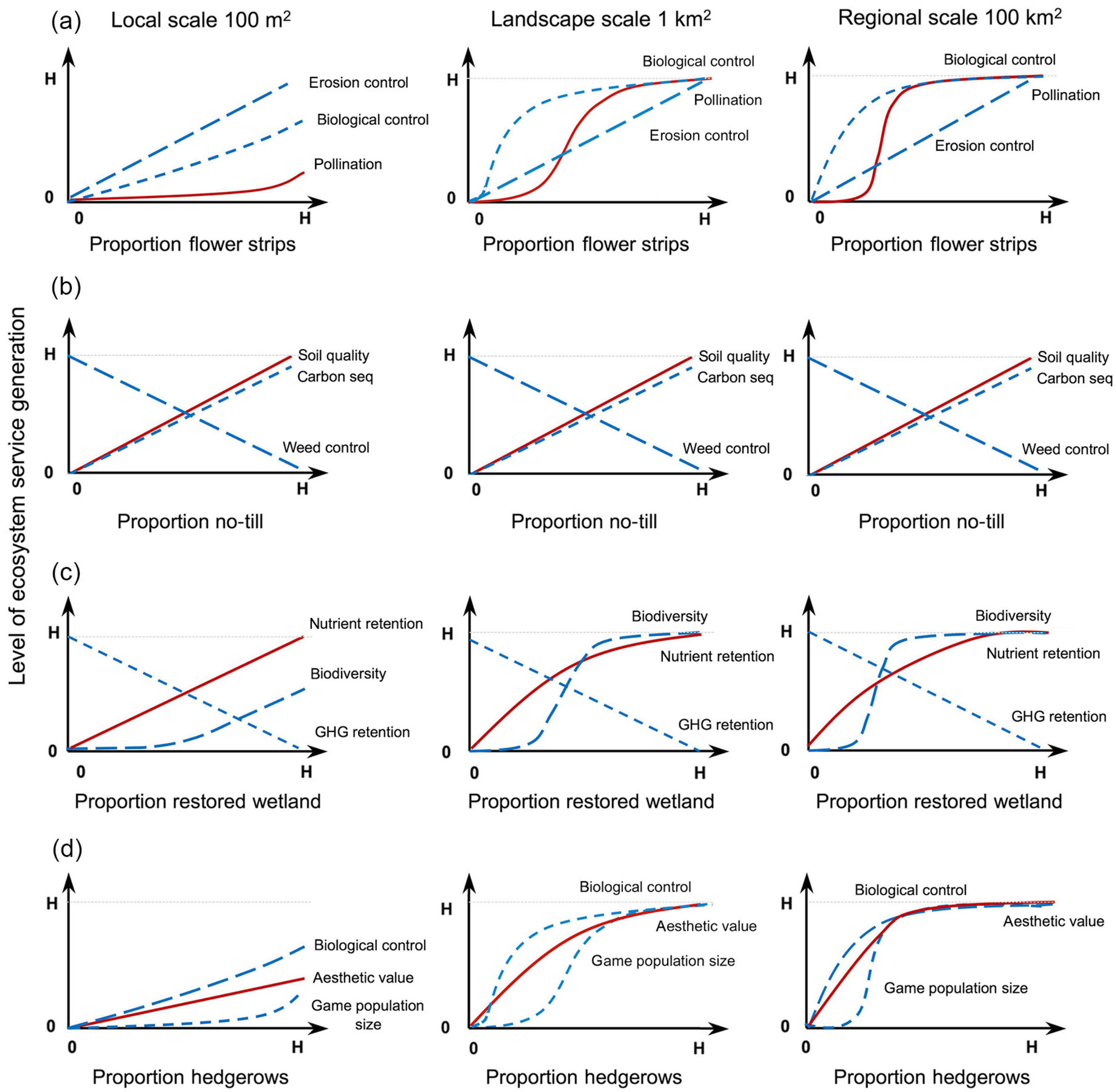

Fig. 2. Management interventions in the agricultural landscape and their hypothetical effect on focal intermediate ecosystem services and potential effects on other interacting services produced in the same landscape. The interventions (a) flower strips, (b) no-till, (c) wetland restoration, and (d) hedgerows are applied at a proportion ranging from 0% to 3% in wetlands and 0% to 10% in others (represented by 0–1 at the *x*-axis) at three different spatial scales: local scale 100 m^2, landscape scale 1 km^2, and regional scale 100 km^2. The level of service generation on *y*-axis ranges from 0 (no service generated) to 1 (hypothetical maximum or saturation point). The relationships assume homogenous landscapes and no previous intervention in the landscape. Focal ecosystem services are represented by the solid line in red and interacting services by the dashed lines.

Hence, we identify four types of response functions that ecosystem services generation at a particular spatial scale might show in relation to the amount of management intervention: linear, exponential, saturating, and sigmoid (Fig. 1).

A linear relationship (Fig. 1a) between the amount of management intervention and the generation of some ecosystem services can be exemplified by the intermediate ecosystem service carbon sequestration that ultimately benefits climate regulation. Given a specific land use and assuming a homogeneous landscape, this service will increase even with few local interventions such as no-till activities (Lal 2004) or grassland management (Soussana et al. 2007), and directly depend on the proportional implementation irrespective of the areal extent (Barford et al. 2001). This is because the ecological processes underpinning carbon sequestration occur at sufficiently small spatial scales in relation to the area at which the management is implemented, while the marginal contribution of the carbon sequestration, when translated into global climate regulation, is sufficiently small to be considered linear and non-saturating.

Many ecological processes will produce non-linear relationships between the amount of management intervention and the generation of some ecosystem services. Some ecosystem services will only be sufficiently produced when the interventions that support them reach a specific threshold level (Fig. 1b). Services such as crop pollination and biological control are population-based ecosystem services (Kremen et al. 2007, Tscharntke et al. 2007, Bengtsson 2010) that depend on the population and community dynamics of the service providing fauna (Jonsson et al. 2014). The local community is a collection of species assembled from a larger-scale biogeographic species pool (e.g., Ricklefs and Schluter 1993, Leibold et al. 2004), and the species in this pool react to changes in their environment at various scales. In a landscape in which a species is absent, because of lack of habitat, an intervention will have to enable that species to achieve a minimum population size before the population is persistent and large enough to provide the service. The ability to reach this minimum population size will depend on the dispersal and colonization capacity of the organisms in question. Note that even if the ecological processes underpinning a service are linearly increasing with the amount of intervention, the final ecosystem services that directly benefit humans can still have non-linear relations with respect to interventions. For example, to provide good water quality, low-intensity water purification is often insufficient, because certain standards for water quality must be exceeded. Hence, our appreciation of water quality is non-linearly related to the additive ecological processes that contribute to water purification (Bennett et al. 2009).

Many ecosystem services will also demonstrate a saturating relationship with the amount of management intervention (Fig. 1c). For example, the marginal contribution to crop pollination when increasing pollinator population will most likely level off at high pollinator population densities (Garibaldi et al. 2011). The amount of intervention at which the relationships reach an asymptote will depend on landscape context, where, for example, the marginal contribution of interventions that benefit pollinators is smaller in a landscape that already is benign to pollinator populations (Tscharntke et al. 2005). Also, human appreciation of ecosystem services may result in saturating relationships. For example, hedges improve the aesthetic appreciation of many western European landscapes, but only up to a certain point (Burel and Baudry 1995).

The combination of thresholds and saturation produces sigmoid relationships (Fig. 1d). Linear, exponential, and saturating responses of ecosystem service generation to management interventions can be viewed as special cases of this more general sigmoid relationship. An example is the effect of flower strips on crop pollination (Blaauw and Isaacs 2014, Feltham et al. 2015). Pollinators may not react to flower strips until flower strips occupy an area that is sufficient to sustain viable populations, and while more flower strips increase the population of pollinators once there are sufficient pollinators, the service of pollination will be saturated. Furthermore, in a complex landscape, pollinators might already be above the inflection point when the management intervention is introduced, resulting in a purely saturating relationship. Similarly, at a very small spatial scale, the relationship between flower strips and pollination may never saturate, resulting in a purely exponential relationship.

Scale-dependent Effects of Management Interventions on Multiple Ecosystem Services

Ecosystem management that increases the production of one ecosystem service sometimes results in unintended declines in the generation of other services (Raudsepp-Hearne et al. 2010, UKNEA 2011, Howe et al. 2014, Kragt and Robertson 2014). For example, management interventions to enhance wood production in forests trade off with wild game production (Gamfeldt et al. 2013), and agricultural production often increases at the expense of biodiversity (Stoate et al. 2009). Negative relationships occur when ecosystem services interact negatively with each other directly, or respond to the same driver in opposite directions (Bennett et al. 2009). The resulting trade-offs and synergies among services can vary depending on the scale at which the intervention and management effort is applied, but such interactions remain largely unexplored. To exemplify how ecosystem service relationships can vary with the amount of management interventions, and how such relationships are modified by the scale (extent) of interventions, we examine four different interventions relevant for agricultural landscapes: flower strips to enhance pollination (Feltham et al. 2015), no-till to improve soil quality (Lal 2004), wetland restoration to improve nutrient retention (Moreno-Mateos and Comin 2010), and hedgerows to improve aesthetic values in the landscape (Burel and Baudry 1995). To explore potential trade-offs or synergies, for each intervention we analyze two additional services potentially directly or indirectly affected by the focal intervention.

To illustrate how the relationships between ecosystem services change with the spatial scale at which interventions are applied, we display hypothetical relationships (Fig. 2) between ecosystem service flows and the quantity of the intervention for three different spatial scales: local (10^{-4}–10^{-3} km^2; =100–1000 m^2), landscape (10^0–10^1 km^2), and regional (10^3–10^4 km^2), and propose how these relationships vary with the scale (extent) of management intervention (Fig. 2). We allowed the amount of the intervention to range from zero to high, where the latter reflects an assumed realistic maximum density at that particular scale. These interventions are introduced into a homogeneous productive agricultural landscape lacking any natural or semi-natural habitats, an assumption that is discussed in the section on how scale considerations can be incorporated into management.

Flower strips—effects on pollination, biological control, and erosion

When introducing flower strips to a landscape to benefit pollinator populations and thus increase pollinator visits to crops, crop pollination will theoretically increase until there is no pollen limitation for seed/fruit set or until food resources for pollinators no longer limit population growth but instead other factors such as nest-site availability (Fig. 2; see *Functional Form of Ecosystem Service—Intervention Relationships*). The increased pollination will have a scale dependence related to the proportion of flower strips. At small spatial scales, it can be more difficult to benefit some species of pollinators because they need a sufficient minimum density of flower strips occurring in the landscape to sustain their populations, assuming that the landscape lacks other flower resources. At larger spatial extents, the pollinators' effect on yield will saturate. An additional ecosystem service potentially enhanced by flower strips is biological control. In contrast to pollination, this service will most likely be positively influenced by interventions already at a local scale, because many biological control agents are less mobile compared to pollinators and hold viable albeit small populations that can benefit from the flower strips (Pywell et al. 2015).

Erosion control tends to increase continuously even at larger scales in contrast to pollination and biological control, which are population-based services that saturate at larger scales. The amount of particles retained in the flower strip vegetation will have an additional increase directly related to the amount of strips irrespective of spatial extent. Habitats with perennial vegetation can also, if well planned, have positive effects on erosion control, especially in steep areas with a high risk for erosion, and thus help to bind the soil with well-rooted perennial vegetation (Hatton et al. 2003, Tyndall et al. 2013).

No-till—effects on soil quality, carbon sequestration, and weed control

No-till agriculture has been suggested as a method to increase yields and organic matter in soils (Smith et al. 1998, Lal 2004). No-till is also argued to increase soil quality by increasing carbon inputs to soil, enhancing earthworm populations and soil structure. The relation between no-till intervention and soil quality is little affected by scale of management (Fig. 2). A linear increase with the proportion of management application of no-till at all scales is expected also for carbon sequestration in the soil (Goldman et al. 2007), thus contributing to climate mitigation at the global scale. A clear trade-off exists, however, between no-till practices and weed control, as weeds are positively affected by less ploughing, resulting in a negative relation between soil quality and carbon sequestration and weed control (Stoate et al. 2009). Hence, an increase in no-till practices within a landscape or a region might lead to greater weed and pest problems in the crop fields, which may increase the use of pesticides or herbicides (Pimentel et al. 1991, Young et al. 2006). In addition, recent studies suggest that the effect of no-till on yield is positive only under certain conditions, and evidence for a general positive effect is equivocal (Pittelkow et al. 2015). Similarly, the positive effects of no-till on carbon sequestration have been questioned (Powlson et al. 2014, Ugarte et al. 2014, Lubbers et al. 2015).

For the present analysis, we nonetheless assume that neither soil quality, carbon sequestration, nor weed control is directly scale dependent (Fig. 2); that is, that there are linear relationships between the proportion of no-till intervention and the selected intermediate ecosystem services generation at all scales. Consequently, no-till agriculture is synergistic with carbon sequestration at all scales. Hence, improved soil quality and climate regulation are both assumed to be supported by no-till management, but trade off with weed control (Nichols et al. 2015).

Wetland restoration—effects on nutrient retention, greenhouse gas retention, and biodiversity

Restoring wetlands provides a saturating enhancement of the ecosystem service nutrient retention (Fig. 2). Some positive effects of wetland restoration will occur at local scales, while larger landscape to regional scales are needed for full synergism with nutrient retention because restoration can be directed to where they are most efficient. Wetlands and riparian buffers are important for filtering, absorbing, and slowing the rate of flow of run-off (Daily and Ellison 2002, Boody et al. 2005). The shape of the curve depends to large extent on how water flows through the landscape as affected by elevation and precipitation, the amount of nutrients in the water body, as well as landscape configuration.

We expect restoring wetlands will produce a sigmoid increase in biodiversity. Restoring wetlands in agricultural areas is positive for biodiversity, but due to population dynamics and dispersal limitations, restoration will be more efficient when performed at larger scales. A landscape must contain a certain area of wetlands or well-connected smaller patches to sustain viable populations (Moreno-Mateos and Comin 2010), similarly as for pollination and flower strips. However, wetlands can also release the potent greenhouse gas (GHG) N_2O (Burgin et al. 2013, Moor et al. 2017), especially if there is a high nutrient load (Verhoeven et al. 2006).

Hedgerows—effects on aesthetics, game population size, and biological control

The addition of hedgerows to a landscape has a scale-dependent and potentially saturating impact on the production of aesthetic services (Fig. 2; Burel and Baudry 1995, Hägerhäll 1999). Hedgerows have also been shown to be beneficial to wildlife and general biodiversity in agricultural landscapes and are supported by subsidies in several countries (Wiens 1992, Burel 1996, Munro et al. 2009, Stoate et al. 2009). Because home ranges and population dynamics of game populations occur at relatively large scales, increasing proportion of hedges at local spatial scales tend to have only small positive effects on hunting. At larger scales, hedgerows may have larger positive effects, possibly leveling off at very large spatial scales as the marginal value of each new hedgerow diminishes (Wiens 1992).

Natural vegetation such as hedgerows could also have a positive effect on biological control (Thies and Tscharntke 1999; Fig. 2). Hence, the addition of hedgerows at a local scale will increase aesthetic values as well as biological control, but have little or no effect on wild game production.

The curves in Fig. 2 suggest that the optimal scale of management differs among services within a landscape as an effect of the scale of ecological processes underpinning service generation. Population-based services like game, pollination, and biodiversity (biological control is less clear) are more optimal to manage at landscape to regional scales as the amount of interventions at smaller scales could be insufficient to sustain viable populations. In contrast, interventions more directly related to soil processes could potentially affect generation of services already at local scales, although the total magnitude of, for example, carbon sequestration increases with the spatial extent of the intervention.

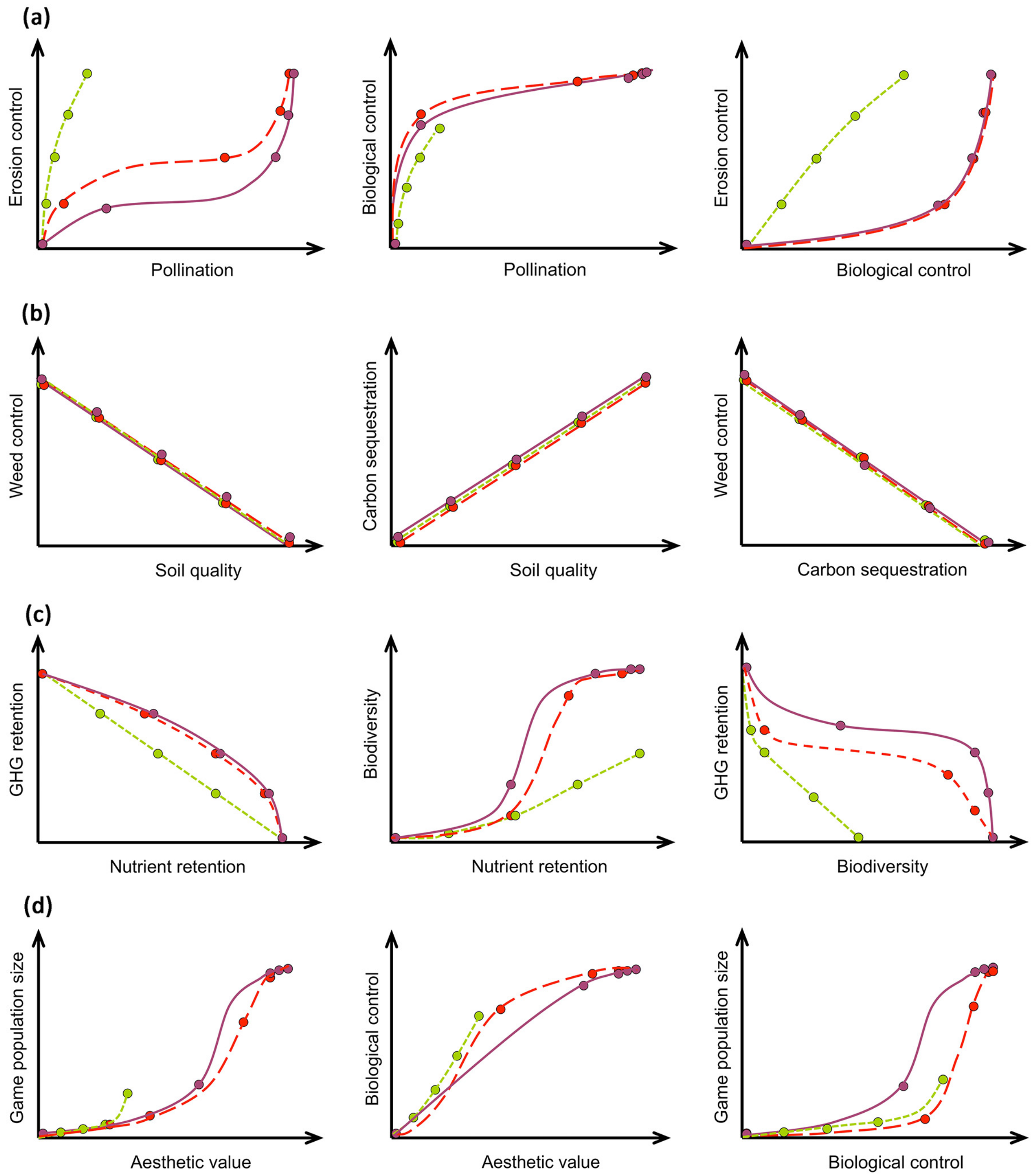

Fig. 3. Hypothetical curves showing pairwise trade-offs and synergies between intermediate ecosystem services at different scales, based on the management intervention effects outlined in Fig. 2. The lines show the curves at different spatial scales: dotted line (green) = local scale; dashed line (red) = landscape scale; unbroken line (purple) = regional scales. The dots indicate values at 0%, 25%, 50%, 75%, and 100% of the intervention at different scales. (a) Non-linear synergistic relations between pollination, erosion control, and biological control in the flower strip intervention case. (b) Linear relations between weed control, soil quality, and carbon sequestration in the no-till case. Synergistic relation between soil quality and carbon sequestration, but trade-offs between weed control and soil quality or carbon sequestration. (c) Non-linear trade-offs between greenhouse gas

(*Fig. 3. Continued*)
emissions and nutrient retention (left) or biodiversity (right), and synergy between nutrient retention and biodiversity (middle) in the wetland restoration case. (d) Non-linear synergies between aesthetic value, game population size (for hunting), and biological control in the hedgerow construction case.

The realistic size of interventions in practice also to some extent determines the scale at which service generation operates. This means that effects neither at micro- nor at macro-scale are reflected in Fig. 2. Hence in theory, also linear relations could turn into sigmoid shapes like Fig. 2d.

Trade-offs and Synergies Between Ecosystem Services

Based on the relations between ecosystem services and scales depicted in Fig. 2, we plotted pairwise relationships between services exposed to different amounts of interventions at different spatial scales (Fig. 3a, d). The resulting plots show the trade-offs and synergies among the services, assuming that the hypothetical relations in Fig. 2 hold. Some pairs of ecosystem services most probably show synergetic relationships; for example, managing for pollination by introducing flower strips is likely to increase erosion control. Other pairs are more likely to show trade-offs. A possible case is that increased nutrient retention of wetlands may be negative for biodiversity, and also risks resulting in increased GHG emissions (Fig. 3c). Hence, it appears that when managing for population-based ecosystem services, synergies become more prominent when interventions are implemented at larger spatial scales, while non-population-based ecosystem services are enhanced irrespective of spatial scale. However, the functional shape of trade-offs and synergies varies when scale changes (Fig. 3).

Our analysis suggests that managing for full capacity for synergies among multiple service is easier to do at larger spatial scales (landscape/region; Fig. 3a, d). Similarly, trade-offs may also be more likely to play out on larger scales (Fig. 3c). In addition, Fig. 3 also suggests that trade-offs and synergies remain similar in direction irrespective of scale as long as relations between service level are positive or negative along the intervention gradient (as in Fig. 2). This means that synergies at one spatial scale do not switch into trade-offs and that trade-offs do not turn into synergies with changed scale of management. However, if other types of relations than in Fig. 2 occur, the relation will change from synergy to trade-off. One example may be when relations are hump-shaped, for example, if predators or parasitoids are added at landscape or regional levels, when the proportion of intervention increases. Although it is premature to suggest that all these patterns will hold in real-world situations, we stress that these analyses provide points of departure for hypotheses to be tested in empirical studies.

Incorporating Scale into Co-management Practices to Enhance Multiple Ecosystem Services

Importance of initial landscape conditions and placement of interventions

To inform management, the suggested relationships across scales and services have to be linked to real landscape conditions. Potential thresholds in relation to the amount of management will depend on the specific ecological context, for example, landscape structure (Tscharntke et al. 2005, Kleijn et al. 2011) and the available species pool (Lindborg et al. 2014), as well as the scale at which the intervention is applied. The marginal value of an intervention will depend on the amount and extent of what is already in the landscape, potentially changing the shape and scale dependence of the curves in Fig. 2. For example, adding a small patch of flower resources in a landscape devoid of other resources to pollinators might be futile, whereas it can have an added value in landscapes that are moderately complex (Scheper et al. 2015). Hence, the sigmoid relationships depicted at small extents (Fig. 2) may turn into saturating responses in intermediately complex landscapes, or even no relationships in very complex landscapes (Tscharntke et al. 2005, Kleijn et al. 2011).

To illustrate the importance of initial landscape conditions (configuration and heterogeneity) for the relation between management intervention (hedgerows, flower strips, wetlands) and

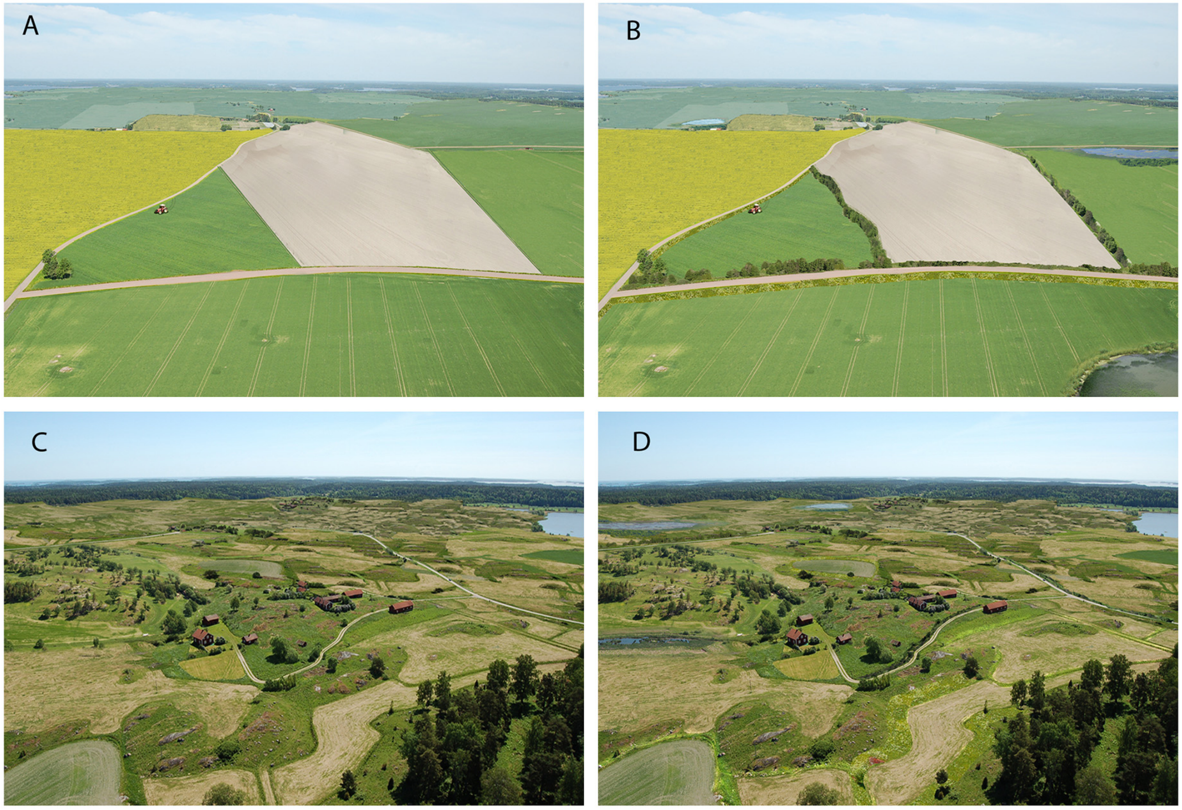

Fig. 4. The effect of management intervention differs depending on the initial conditions (configuration and heterogeneity) of an agricultural landscape, here illustrated as two types of landscape with or without the interventions: hedgerows, flower strips, and wetlands. (A) A cleared landscape with no/few natural habitats; (B) is the same landscape as (A), but with added interventions; (C) a landscape with some natural habitats occurring; and (D) is the same landscape as (C), but with added interventions. In landscapes (B) and (D), the same amount of interventions is added: 500-m hedgerows, 500-m flower strips and three wetlands. The photographs were manipulated in Adobe Photoshop (cf. Lindborg et al. 2009 for details).

ecosystem service generation, we depict two contrasting agricultural landscapes at different ends of a landscape heterogeneity gradient (Fig. 4). The landscape in Fig. 4a is highly modified and intensively used and contains few natural habitats. In such landscapes, the introduction of interventions (Fig. 4b) may still support service providing species present in the limited species pool (Rundlöf et al. 2008), increasing service provision from a very low level. In the heterogeneous landscape in Fig. 4c, there will, in contrast, be limited influence of interventions (Fig. 4d), because such landscapes support a large species pool which contribute to high species richness everywhere, independent of interventions (Weibull et al. 2000). For many scale-dependent services, interventions in an intensively used simple landscape (Fig. 4b) may have positive but delayed effects as species need to respond to the intervention by increased populations (Kleijn et al. 2011). Hence, the same amount of interventions could have different relative effects depending on the grade of heterogeneity. This means that, in the sigmoid relationship between ecosystem services and management interventions (Figs. 2, 3), the intercept and inflexion points will differ depending on initial landscape conditions. In a heterogeneous landscape (Fig. 4d), the intercept will be higher than in homogeneous (Fig. 4b; cf. Tscharntke et al. 2005), but the effect of a certain amount (proportion of area) of interventions can also be smaller. The effects of interventions on saturating functions such as nutrient retention or aesthetic values (Fig. 2) will also be affected by the initial landscape configuration to which they are implemented. Also, services that at some scales increase exponentially with proportion of intervention, such as erosion control, will need fewer interventions at local and landscape scale for the same level of service to be generated if the landscape already contains habitats that benefit these ecosystem services, for example, perennial vegetation that stabilizes soil (Fig. 4d).

The theoretical relation between amount and extent of interventions suggests that the full capacity for multiple service synergies is easier to manage for at larger scales (Fig. 3). At those scales, landscape configuration is easier to account for which enables more optimal placement of interventions compared to interventions at local scales. For example, if the same amount of flower strips is introduced at larger scales in Fig. 4c, they can more easily be optimally placed in relation to other nectar-supplying habitats (Kleijn and Sutherland 2003). Scale-invariant responses to management interventions are rarely affected by landscape configuration, but will be directly affected by management intensity and location of intervention. Soil quality, carbon sequestration, and nutrient retention are all highly dependent on the placement of the intervention and will be indirectly affected by landscape elevation or up-stream–down-stream location.

An interesting consequence of effects of heterogeneity in a landscape is plausible thresholds and hysteresis effects in the management of ecosystem services (Gordon et al. 2008). There are, for example, time delays in the response of organism groups to changes in management (Jonason et al. 2011), which means that once species or ecosystem services are lost from a landscape, a substantial amount of interventions may be needed for recovery (Kleijn et al. 2011). It has been shown that applications of agri-environmental schemes are not always successful in intensively farmed agricultural landscapes because of lack of population source patches from which the habitats created by the schemes can be colonized (cf. Tscharntke et al. 2005, 2012) or too few nutrient retention areas (Gordon et al. 2008). For population-dependent services, it also implies that ecosystem services can be maintained in degrading landscapes for a longer time than expected due to slow turnover time and population persistence in at least some remnant patches (Eriksson 1996, Lindborg and Eriksson 2004, Kuussaari et al. 2009). The potential existence of thresholds complicates traditional approaches trying to optimize production, and suggests that management should balance production with approaches that build resilience (Peterson et al. 2003, Fischer et al. 2009, Biggs et al. 2015).

Coordinated management

The need to merge ecological and socio-economic aspects of who is benefiting from ecosystem services, and where, has been recognized (e.g., Polasky et al. 2005, Pushpam 2010). Most plans for ecosystem services management focus on small local sites and fail to consider how this individual local focus will produce ecosystem services at the landscape scale (Ghazoul et al. 2009). We stress that the scale at which ecosystem services are managed often needs to be the landscape, that is, in agricultural landscapes involving large single or multiple neighboring farms.

The optimal scale of management also differs among services within a landscape as an effect of the scale of ecological processes underpinning service generation. Hence, to effectively produce a service, the scale of management must match the scale of ecological processes contributing to ecosystem service generation. For example, a service like pollination may require coordinated actions among neighboring farms to be efficiently enhanced (Stallman 2011, Cong et al. 2014). For other intermediate services, the spatial scale underpinning the service may be sufficiently small that no particular benefit occurs from collaboration between farms. This is the case for carbon sequestration that when translated into climate regulation will become a public good at a global scale. For both pollination and climate regulation, the mismatches between scales of management and scales of benefit of ecosystem services can result in services becoming both underprovided (tragedy of ecosystem services) and overused (tragedy of the commons; Lant et al. 2008).

Our results not only suggest that voluntary collaboration between stakeholders can be beneficial, but also that collaboration should be encouraged by ecosystem service governance. The major instruments to promote biodiversity in European agricultural landscapes are agri-environment schemes, but their success in promoting biodiversity is debated (Kleijn et al. 2011, Peer et al. 2014). These schemes could potentially also promote ecosystem services (Hauck et al. 2014), requiring management at the landscape scale (Prager et al. 2012, Galler et al. 2015). Possibilities to support such larger-scale management include collaborative mechanisms (McKenzie et al. 2013) or agglomeration bonuses (Drechsler et al. 2010).

Problems associated with scale challenge the management of ecosystem services. This is due to variation in both the scales at which ecosystem processes operate and the spatial relationship with management. In this paper, we provide a first step in guiding empirical and theoretical research to understand the underlying complexity of scaling for generation of ecosystem services to inform management of services in real landscapes. To enhance service generation and minimize scale-dependent trade-offs, scale mismatches due to differences in underpinning ecological processes should be recognized to ensure coordinated actions in each given landscape context.

Acknowledgments

This paper was initiated during a workshop organized and financed by Stockholm Resilience Centre in the Freshwater, Food and Ecosystem Service research theme. We thank O. Eriksson, E. Andersson, R. Rader, and two anonymous reviewers for valuable comments on earlier comments on the manuscript, and J. Lindborg for photo manipulations. Financial support was provided by the Swedish Research Council FORMAS to the research projects SAPES and MULTAGRI, by the EU 7th Framework Program to the Project LIBERATION (Grant 311781).

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